

ASPECTS OF THE LIFE HISTORY OF *CARCINONEMERTES ERRANS*
(NEMERTEA: CARCINONEMERTIDAE), AN EGG PREDATOR
OF THE CRAB *CANCER MAGISTER*

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The nemertean genus *Carcinonemertes* has been known for over a century as an epibiont of brachyuran crabs. Even though symbiotic life styles are highly unusual for nemerteans, only a limited amount of research has been devoted to the study of *Carcinonemertes*. Worms of this genus infest crabs after a planktonic larval stage. They next remain dormant, encysted on the host's exoskeleton. Worms on female hosts migrate into the host egg clutch when it is oviposited for brooding under the abdomen. There they grow, mature, and lay their own eggs.

While the basic outline of the life history of *Carcinonemertes* has long been known, it was only recently confirmed as a predator of its hosts' eggs (Wickham, 1978). Earlier workers had suspected that *Carcinonemertes* was an egg predator, but never actually observed feeding (Humes, 1942; Kuris, 1971). The worms have been considered generalists in terms of host specificity. But little is known of the extent to which *Carcinonemertes* is capable of affecting host population dynamics.

Carcinonemertes errans Wickham is the first of these worms found to be specific to a single host species: the commercially important Dungeness crab, *Cancer magister* Dana. This worm recently was found to exist at epidemic levels on the Central California Dungeness crab population (Wickham, 1979a). The egg mortality it has caused in this region is high enough (averaging over 50% of the eggs produced annually) to implicate this worm in the collapse of the Central California Dungeness crab fishery. *Carcinonemertes* occurs on a large number of ecologically and economically important brachyuran crabs, and is now known to be capable of having a significant effect on its hosts' reproductive output. The following study on the life history of *C. errans* was initiated for this reason.

MATERIALS AND METHODS

Aspects of the life history of *C. errans* were studied in both the laboratory and the field. Worm abundance in the field was investigated using crabs caught in trawls and traps at Bodega Bay and Eureka, California. These crabs were dissected and all worms observable were counted and their locations on the exoskeleton noted.

Samples also were obtained from the egg clutches of ovigerous female crabs by fishermen in the field. Sampling was done by inserting forceps into the egg clutch approximately at the middle of the exposed portion of the clutch. Care was taken to insert the forceps deeply enough to remove complete egg-bearing setae. The egg samples obtained contained an average of approximately 100 egg-bearing setae which each held about 200 eggs. Dungeness crabs carry up to 2,500,000 eggs in a clutch, so these samples were approximately 1% of the clutch. The egg samples were placed in vials with a 5% formalin sea water solution and examined later with a dissecting microscope.

During examination of the samples all worms were removed and counted. Worm egg strings, which are laid among the crab eggs, were also counted and a portion removed for weighing. The number of crab eggs in each sample was computed by removing a subsample of 10–15 crab-egg setae and counting all live and dead eggs. Percent egg mortality was computed from this and the subsample was dried and weighed to compute the weight per egg. The rest of the sample was then dried and weighed and the weight per egg used to estimate the total number of eggs in the sample. Worm population density was expressed as worms per 1000 crab eggs. Number of worms per host was computed for egg samples obtained from crabs which had been measured for carapace width at the time of sampling. Egg clutch size was estimated for these crabs from the size fecundity curve for the Dungeness crab (Botsford and Wickham, 1978) and worms per 1000 eggs were then used to compute total worms percent in egg clutches.

The actual age of worms present on crabs was unknown, since it was impossible to tell when specific worms infested their hosts. Maturity and essentially all growth of worms living on hosts occurs during the host's egg-brooding period, so the chronology of growth and reproductive processes depends on the number of days worm populations spend in the host's egg clutch. Most worms on hosts migrate to the egg clutch within a day or two after host oviposition, so worm age was expressed as the same age as the crab embryos. Age of crab embryos was estimated by comparing the development of eggs in a sample with descriptions of embryos obtained from crabs sampled throughout their brooding period in the laboratory.

Dry weight of worm populations in egg samples from individual hosts was measured and the average weight per worm computed. Worm fecundity was measured by weighing worm egg strands in the samples. A counted sample of 20,000 worm eggs was dried and weighed to determine the weight per egg and this figure was used to compute the number of eggs per strand. Isolated worms were reared in 100-ml jars with approximately 1000 crab eggs for food until they laid their own eggs, to determine how many egg strands each worm laid in a single host's brooding period. The ratio of worm egg strands to worms was computed from field samples to determine when in the host's brooding period worms produced eggs.

Worm distribution with a host egg clutch was determined by measuring the distance of worms from the tip of the host's egg setae. Distribution of worm egg strings in the host egg clutch also was determined in this fashion.

RESULTS

Early life history

Worm larvae hatch from an egg strand laid among the host eggs. The larva is a simple ciliated ellipse about 100 μm in length, with anterior and posterior apical tufts of what appear to be sensory setae. Upon hatching it immediately swims into the water column and after a few hours begins to alternate crawling on the container bottom with swimming.

Crabs first begin to carry worms after they reach a carapace width of 20 mm (Fig. 1). Worm numbers increase with crab size.

Juvenile worms remained alive for as long as 6 months in finger bowls even though no food was added. The sites of juvenile worm infestation differed between

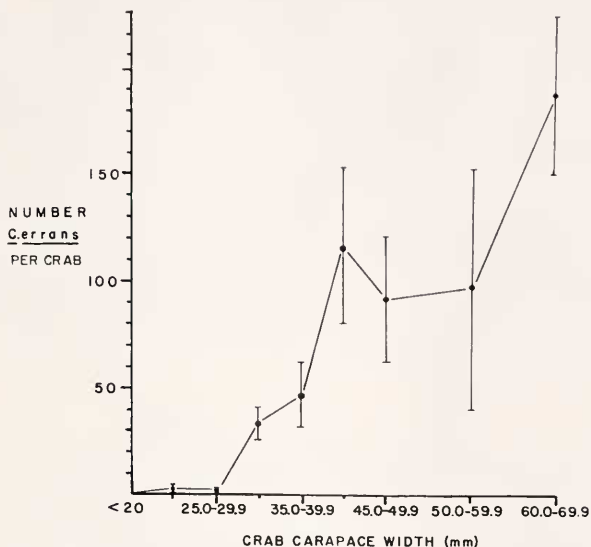


FIGURE 1. Number of *Carcinonemertes errans* per crab (\pm s.e.) from newly settled juvenile crabs in Bodega Bay, California. N = 59 crabs.

male and female hosts. Dissection of mature, non-ovigerous female crabs revealed worms in virtually every protected crevice or joint on the animal. Areas on the carapace lined with setae harbored large clusters of mucus-covered worms. Groups of worms which, while topologically external, appeared to be internal, could be found in the invaginations of the apodemes. Worms were among the mouth parts, and large populations were found in the eye sockets and on the bases of the eye stalks. The average number on this group of 11 females was 15,011 worms. Some of the sites occupied on these crabs might not be infested at lower densities.

On mature male crabs, the major site of infestation was beneath the abdomen, with concentration often at its base or on the copulatory appendages, although some worms were found elsewhere.

More than 90% of the juvenile worm population on one mature male crab which molted in the laboratory sometime at night had moved off the exuvium onto the new soft exoskeleton by morning.

Host oviposition and C. errans trophic period

Juvenile specimens of *C. errans* leave the host's exoskeleton and move into its egg clutch within 1-2 days after oviposition. Worms begin to feed on host eggs within a day of entering the egg clutch.

During the early period of the crab's brooding, worms spend most of their time at the periphery of the egg clutch. Worms are concentrated near the tips of individual egg setae during the first 40 days of host brooding. As they mature they distribute themselves more evenly (Fig. 2).

Feeding *C. errans* move freely about the host egg clutch during the host's entire brooding period. They do not secrete a sheath as do all other described species of *Carcinonemertes*.

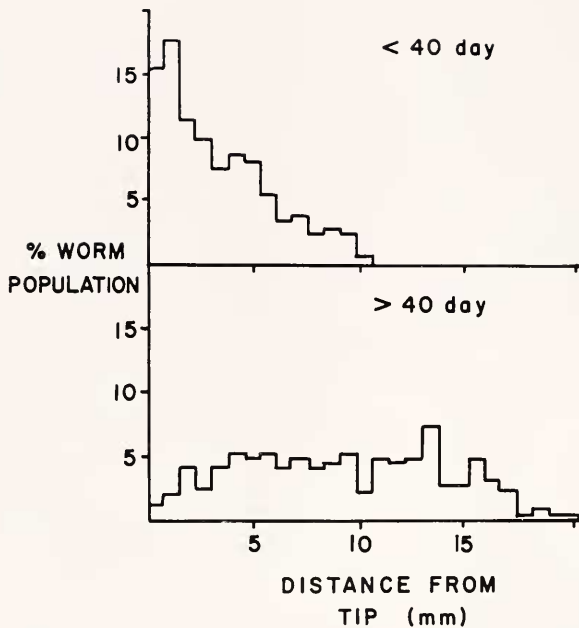


FIGURE 2. Distribution of *Carcinonemertes errans* along crab egg setae for broods less than and greater than 40 days of development. $N = 884$ worms, < 40 days; 851 worms, > 40 days.

Worm growth

Juvenile worms remain approximately 0.5 mm in length while on the host's exoskeleton. The worms grow only during their feeding period in the host egg clutch. Average worm weight increases slowly through the first 40 days of host brooding but then begins to increase more rapidly during the second half of the ovigerous period (Fig. 3).

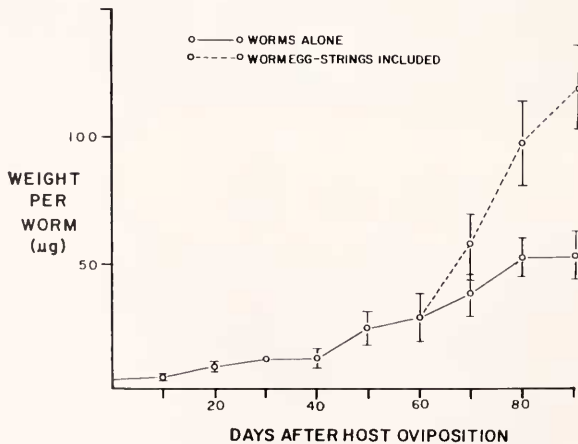


FIGURE 3. Average weight of *Carcinonemertes errans* (\pm s.e.) as a function of age of their host egg clutch. Dashed line includes the weight of the worm egg strings on a per worm basis. $N = 196$ crabs.

The worms' growth appears to be sensitive to their densities within individual host egg clutches. Analysis of samples of similar age for the relationship of average worm weight to density shows that most of the decrease in growth rate occurs as density increases to about 10 worms/1000 crab eggs (Fig. 4).

The appearance of *C. errans* changes as growth and maturity proceed. The sizes of the proboscis chamber and the stylet remain constant (stylet about 50 μm in length) throughout life on the host. As female worms begin to increase in size their epidermises become more transparent as the white spots in the epidermis separate, eventually allowing the gut pouches to become visible along the sides. Female worms take on a segmented appearance when mature, due to the alternation of ovaries and lateral outpockets of the gut. Eggs are fertilized internally and become visible through the epidermis at maturity.

Worm reproduction

Copulation by specimens of *C. errans* was never observed; however, worms are found aggregated in clusters or in pairs from about 20–40 days after host oviposition. Copulation may occur during this period, since several female worms isolated 30 days after host oviposition with approximately 100 crab eggs for food produced fertile eggs.

Worms begin laying eggs after 65–70 days in the host egg clutch. Eggs are laid in a cylindrical gelatinous matrix which is wrapped around the host egg string. Worm egg strands can be found attached all along the host egg setae but are less frequent near the tips at the periphery of the egg clutch (Fig. 5).

Fecundity of *C. errans* is variable and appears to be density dependent. Worms held in the laboratory exhibited high variability in both the number of egg strands produced and the number of eggs per strand (Table I).

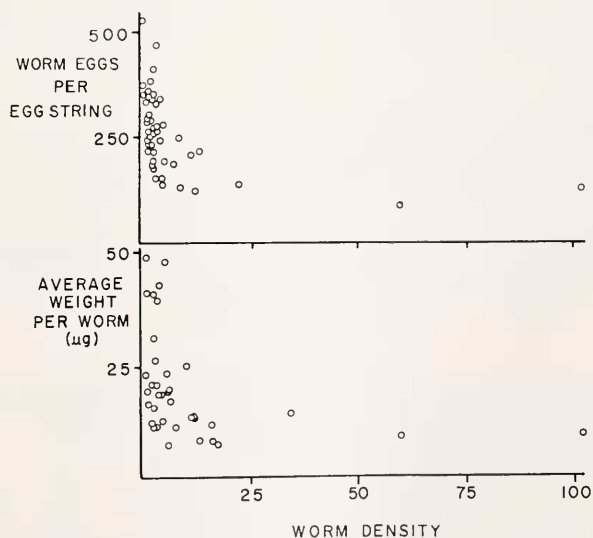


FIGURE 4. Number of worm eggs per egg string and average weight per worm of similarly aged samples as a function of worm density in the egg clutch (worms per 1000 crab eggs). $N = 46$ samples for eggs per string, $N = 37$ samples for average weight.

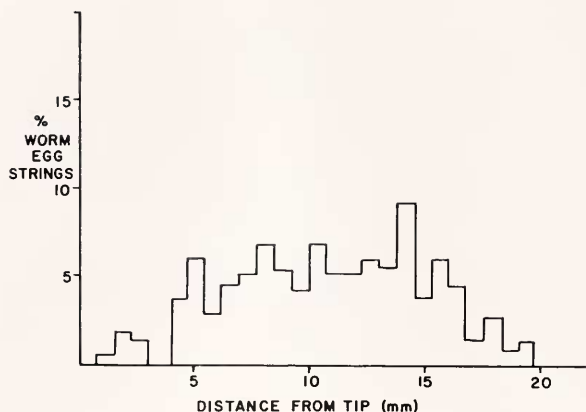


FIGURE 5. Distribution of egg strings of *Carcinonemertes errans* along host egg setae. $N = 213$ worm egg strings.

Total fecundity per worm declined as the number of worms in 100-ml jars increased, for a limited number of samples (Fig. 6).

In field samples the ratio of worm egg strands to worms ranges up to 7.12. The average was 1.92 egg strands per worm in 73 samples of crab eggs in their last 10 days of development (more than 80 days after host oviposition). The average number of eggs per strand, based on weight measurements of 2500 egg strands, was 265. In these samples the number of eggs per strand declined with density, with most of the decline occurring at the lower densities (Fig. 4).

Infestation rates

Carcinonemertes errans differs from other congeners, being present on over 98% of all potential hosts. All non-egg-bearing crabs above 20 mm carapace width in the Bodega Bay area in Central California had worms. Similarly, only 10 samples from crab egg clutches out of more than 500 collected over a 5-year period contained no worms.

Worm density (worms per 1000 crab eggs) in samples varied from 0 to 101.8 in one sample collected outside San Francisco Bay. Average worms per 1000 crab eggs for seasonal crab-egg collections from Pacific coast localities varied from a low of 0.66 in Alaska in 1979 to 25.41 just outside San Francisco Bay in 1977/78 (Table II). Worm density per crab in those collections in which the size of the crabs was measured varied from 1430 in Alaska in 1979, to 20,580 in Washington in 1978/79. Using the average fecundity of the measured crabs it was possible

TABLE I

Number of egg strands produced by worms in the laboratory. The number of egg strands per worm and total fecundity data are based on average values per container. Individual fecundity could only be measured in jars with single worms. $N = 29$ worms.

	Egg strands per worm	Eggs per egg strand	Fecundity per worm
Average	3.1	446	1339
Range	1-8	79-1409	847-4784

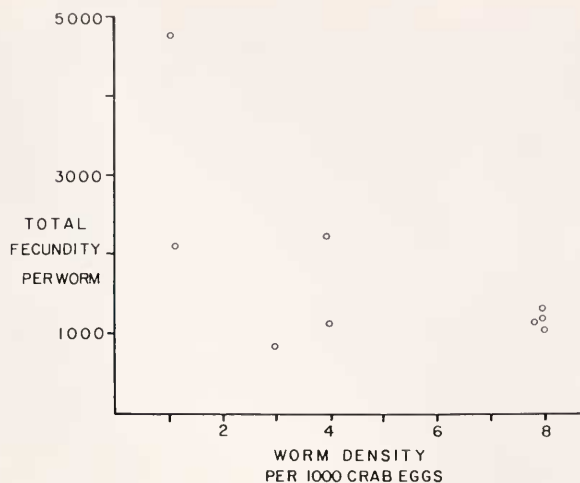


FIGURE 6. Fecundity per worm for *Carcinonemertes errans* held in 100-ml jars at various worm densities. N = 9 samples.

to estimate an average of 43,026 worms per crab outside San Francisco Bay, in 1977/78.

DISCUSSION

The larval life of *Carcinonemertes* is poorly known. Based on the timing between maximum hatching and maximum recruitment to hosts by *C. epialti* on the host *Hemigrapsus oregonensis* by Kuris (1978) and Roe (1979) the larval life

TABLE II

Average worm densities (worms per 1000 crab eggs) for yearly samples along the Pacific coast of North America along with coefficients of variations in density and projected average crab egg mortality from the sampled populations.

Sample collection	Number of samples	Mean worm density	Coefficient of variation	Mean worms per crab (for measured crabs)	Projected % crab egg mortality
Eureka					
1974-75	32	1.78	182.0%		10.6
1975-76	41	4.98	1177.3%		28.5
1977-78	50	4.03	221.1%		30.0
1978-79	35	5.90	425.8%	6901 12,049	43.9
San Francisco					
1974-75	37	14.59	886.6%		63.3
1975-76	86	8.56	1070.9%		50.3
1976-77	44	10.02	823.9%		45.1
1977-78	48	24.96	2905.5%		62.5
1978-79	33	7.76	542.1%		44.6
Washington					
1975-76	16	2.25	338.7%	4647	15.9
1978-79	19	11.14	265.4%	20,580	61.2
Alaska					
1978-79	30	0.66	125.8%	1430	7.6

of this worm species appears to be about 8 months. Juvenile *C. errans* were not found on young-of-the-year Dungeness crabs until August or September, when the newly settled hosts exceeded 20 mm carapace width. Older crabs carried too many worms to accurately count and worms could settle on them at any time during the year. But the worms arriving on young-of-the-year crabs have to be at least 8–9 months old, having hatched the previous December or January at the end of host brooding. *Carcinonemertes* appears to have a relatively long larval period when compared to many other planktonically dispersed marine invertebrates.

Worm numbers increase with crab size during the first few months of the crab's benthic existence. This increase appears to occur throughout the host's life, since adult crabs could accrue in excess of 100,000 worms. Kuris (1978) found a similar increase of *C. epialti* on *H. oregonensis* of increasing size. Since *H. oregonensis* sheds its worms at molting, he proposed that worms settle continuously during the host's intermolt period and larger numbers occurred on larger crabs due to their longer intermolt periods.

Recruitment to hosts by *C. errans* differs from *C. epialti*. *C. errans* juveniles move from the exuvium to the new exoskeleton when the host molts, so hosts can acquire increasing numbers throughout their lives. P. Roe, J. Crowe, L. Crowe, and D. E. Wickham (in preparation) demonstrated that juvenile *C. errans* actively absorb dissolved primary amines from sea water and that leakage of amines across the uncalcified portion of the host's exoskeleton appears sufficient to meet dormant worms' metabolic needs. It is possible that worms arriving on a female host may remain for several years until the host broods eggs.

The sites of infestation by juvenile *Carcinonemertes* on Pacific coast hosts differ from those described on Atlantic hosts by Coe (1902) and Humes (1942). Individual specimens of *C. carcinophila* on the Atlantic blue crab, *Callinectes sapidus*, are found encysted between the gill lamellae on non-ovigerous hosts. Hopkins (1947) found that these worms could move back and forth from gills to egg clutches through the summer, since *C. sapidus* no longer molts after maturity and produces several broods during the summer. *Carcinonemertes* can reach a length of more than 70 mm on blue crabs, compared to a maximum of about 10 mm on Pacific coast hosts, which brood only once a year.

Feeding by *C. errans* begins when female Dungeness crabs oviposit their broods during October and November. This host carries up to 2,500,000 eggs for a period of approximately 90 days. *C. errans* juveniles move into the egg clutch a day or two after host oviposition.

During its period in the host egg clutch *C. errans* differs from all other described *Carcinonemertes* in the lack of a sheath. Members of other species secrete a mucous sheath in which they live. Often males and females will be found together in these sheaths. *C. errans* remains free-crawling while on host eggs, secreting copious quantities of mucus, apparently for adhesion.

All measurable growth of *C. errans* occurs during its period in the host egg clutch. Wickham (1979b) found that the average size of worms within a population from a single host was correlated with the number of crab eggs eaten per worm on that host. Female worms are larger than male worms. However, the opacity of the epidermis in *C. errans* makes sex determination more difficult than in other local species which are more transparent.

Worm eggs hatch near the time of host eclosion and the worm larvae become planktonic. They remain so in the laboratory for at least one month. Thus it is

unlikely that they reinfest the parental host as suggested for *C. carcinophila* by Humes (1942).

The density-dependent decline in fecundity found in laboratory-reared worms and the decrease in size of worm egg strings in field samples correlate with the decline in feeding and growth (Wickham, 1979b). This decline may reflect the action of some form of active intraspecific interference by *C. errans*. It occurs before food resources appear to be limiting, since in the test tube cultures crab egg mortality never exceeded 4%, even in tubes with eight worms.

Carcinonemertes errans is so far the only described species of *Carcinonemertes* restricted to a single host. *C. carcinophila* has been described from 26 host species in the Atlantic, Caribbean, and Mediterranean (Humes, 1942; Kirsteuer, 1966; Vivares, 1975; Norse, 1975). *C. epialti* has been described on nine hosts (Humes, 1942; Kuris, 1978; Roe, 1979) and *C. mitsukurii* from five hosts ranging from Japan to the Indo-Pacific and Hawaii (Humes, 1942). Wickham (1978) indicated that morphological characteristics in the sheaths of the other locally occurring *Carcinonemertes* spp. suggest that host specialization in this genus is more common than previously thought.

The biology of *C. errans* appears to adapt it specifically to its host. The fact that it was never found on alternate hosts such as *Cancer gracilis*, which shares the habitat of the Dungeness crab, suggests an ability to recognize its host. Its ability to transfer from the old exoskeleton during molting suggests a sophisticated behavioral repertoire, and the differential distribution on male and female exoskeletons shows an ability to discern the sex of the host.

Timing of development during the worm's trophic period appears to be an important adaptation in *C. errans*, especially when compared to worms on other hosts. *C. errans* matures and lays its eggs within about 2 weeks of the end of the host's brooding, after 65–70 days on the egg clutch. The time of development to worm hatching was not measured, but hatching was found to occur usually just prior to and during host hatching. This arrangement of timing would appear to allow worms the maximum amount of time for feeding on host eggs. Kuris (1978) and Roe (1979) found a similar synchronicity in the development of *C. epialti* on the host *H. oregonensis*.

Egg predators abound in nature (Orians and Janzen, 1974), but few specialize to the extent that *Carcinonemertes* does. The lifestyle of this genus shares features with parasitic castrators; however, *Carcinonemertes* is a true predator since it eats several distinct prey individuals during its life (Kuris, 1974).

The widespread occurrence of *Carcinonemertes* on numerous species of brachyuran crabs, many of great ecological and economic significance, gives these nemertean an important role in benthic marine communities. This role is only beginning to be unraveled and the interaction of these worms with their hosts should provide stimulating material for a wide variety of studies on the adaptation of organisms to specialized environments.

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SUMMARY

1. Specimens of *Cancer magister* below 20 mm carapace width are not infested by *Carcinonemertes errans*. Worms infesting young-of-the-year crabs beyond this size would have been in the plankton for 8–9 months prior to host infestation.

2. Nemertean burden on crabs increases with the crab's time on the bottom, at least through the crab's early life. Worms move from the host's exuvium to its new exoskeleton upon host molting.

3. Juvenile specimens of *C. errans* were localized under the abdomen, near the copulatory appendages on male crabs. Juvenile worms were found in protected spots all over female crabs' exoskeletons.

4. Nemerteans migrate to the host egg clutch within a day or two of host oviposition. They are peripherally distributed in the egg clutch through the early part of host brooding, but descend into the clutch to become more evenly distributed in the latter part of the brooding period.

5. All measurable growth occurs during *C. errans*' feeding period in the host egg clutch. Growth is inhibited as the density of worms per egg clutch increases.

6. *Carcinonemertes errans* matures approximately 60–70 days after host oviposition. Worms lay an average of 3.1 egg strings in the laboratory, each containing an average of 446 eggs. Fecundity per worm declines as worm density within the host egg clutch increases.

7. More than 99% of all specimens of *C. magister* are infested by *C. errans* in California waters. Numbers per host can range as high as 100,000.

8. Worms exhibit a contagious distribution among hosts, with the variance in density per host in excess of the mean density in all sample collections. The ratios of variance to mean increase as mean density increases.

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